

CHEMOSYSTEMATIC NOTES ON THE ASTERACEAE. III.

NATURAL SUBDIVISIONS OF THE VERNONIEAE.

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The Vernonieae, a mostly pantropical tribe of Asteraceae containing about 1500 species, is often treated as scarcely more than a series of minor elaborations of a large "core genus" *Vernonia*. Previous subdivisions at subtribal and generic levels have depended primarily on pappus form or on dispositions of heads in the inflorescence, characters that are convenient but not necessarily reliable at the level which they were used. Newer data on chromosome numbers (Jones, 1977) and chemistry (Harborne & Williams, 1977) have prompted some speculation, mostly regarding separate trends in American and Old World *Vernonia*. Pollen structure (Stix, 1960; Jones, 1979; Keeley & Jones, 1977, 1979; and Robinson, 1980a, 1980b) has been used primarily in correlation with species groups within genera. Thus, subtribal concepts in the Vernonieae have remained mostly artificial, and in recent treatments they have tended to be ignored (Jones, 1977). Collecting efforts by the third author of the present paper, and chemical analyses from the second author, have provided much new information for the tribe, and a better basis is sought here for the interpretation of this data. A partial synthesis of available chemical, cytological, and structural data leads to the following phyletic and taxonomic conclusions.

The present study is based on a more complete personal knowledge of the New World members of the tribe. A number of comparatively recent useful treatments also are available for the region, Jones (1973, 1976, 1979b), Jones and Faust (1978), Clonts and McDaniel (1978), and Nash (1976) for various areas of North America, Mexico, and Guatemala; Keeley (1978) for the West Indies; Aristeguieta (1964) for Venezuela; Cabrera and Vittet (1961), Robinson (1979a, 1979a, 1980a, 1980b, 1980c, 1980d), and Robinson and King (1979) for Brasil; and Cabrera (1944) for Argentina. Some useful recent works on African species have been consulted including Adams (1963) for tropical West Africa; Wild (1978a, 1978b) and Wild and Pope (1977a, 1977b, 1978a, 1978b) for south-central Africa; and Smith (1971) for the "Stengelioid species".

Some generalizations are possible regarding the pollen variations in the Vernonieae. There is a tendency for lophorate grains in the tribe, and even the less specialized grains, the

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Lycopodium-type of Stix (1960) or Type A of Keeley and Jones (1979) have a somewhat uneven distribution of spines which suggests rudimentary lacunae. It is presumed here that some tendency toward lophorate grains is basic to the tribe. The simple *Lycopodium*-type pollen is undoubtedly ancestral in the tribe, as suggested by Keeley and Jones (1979), and it is found in most of the groups recognized here at the subtribal level. In both *Polypodiaceae* and *Mosses* there are pollen grains with well-defined lophorate patterns, but in these the ridges are low as in the *Lycopodium*-type, and these seem to be derived directly from that type with no relationship to more specialized lophorate patterns in the tribe. More specialized forms of lophorate pollen occur in members of the subtribe Vernoniinae where they seem to be derived from the basic *Lycopodium*-type that is found in the more primitive members of that subtribe. The subtribes Elephantopodinae and Rolandrianae, which have exclusively specialized lophorate forms of pollen, are here considered derived from the subtribe Vernoniinae.

The Liabeae are treated by some recent authors as a part of the Vernoniaceae (Turner & Powell, 1977; Jansen & Stuessy, 1980). The Liabeae are related to the Vernoniaceae and such a placement is an improvement over the traditional placement in the Senecionaceae. However, the Liabeae are a distinct group with many characters violating the limits of the Vernoniaceae including the basically opposite leaves, the often trinervate venation of the leaf blades, the presence of latex in some members of all three subtribes, the presence of heterogamous heads with rays, and the pollen that is never lophorate. The tribe has distinctions equivalent to those of other tribes related to the Vernoniaceae such as the Mutisieae and Cynareae. The chemistry of the Liabeae is not definitive, showing mostly widely distributed compounds. Still, no complex germacranolides have been found such as are common in the Vernoniaceae.

The following subtribes are recognized in the Vernoniaceae.

PSEUDOSTIFFTIIINAE subtribus nov., E. Robinson, R.M. King, & F. Sahlmann

Plantae fruticulosae vel subarborescentes; folia obovata apice truncata vel leniter retusa. Inflorescentiae thyrsoides-paniculatae. Capitula uniflora; squamae involucri interiores facile deciduae; corollae subcarnosae 12-13 mm longae 3-lobatae in lobis erectae vel incurvatae; cellulae endotheciales anguste ellipticae in parietibus transversalibus angustis plerumque 1-3-nodatae; scapi stylorum superae et rami stylorum incrassati carnosae breviter scabri; setae pappi leniter inaequales non dimorphae. Grana pollinis non lophorata valde spinosa in diametro ca. 70 μ m.

Type genus: *Pseudostifftia* E. Robinson

The single genus and species is known only from the interior of Bahia, Brazil, an area of many notable endemics. The genus has been placed in the Vernoniaceae with reservations (Robinson,

1979b). The plant falls generally under the tribal description and does not fit within any other described tribe, but the thickened style with scabrid surfaces and the large non-lophorate pollen grains are unlike any other member of the Vernoniaeae. The elongate endothelial cells with few nodular thickenings are also unusual, but a similar form has been seen in the genus *Aderon* Dalz. of the Vernoniaeae from the region of India.

Chemical analysis of *Pseudostictia* has indicated mostly polyacetylenes, triterpenoids, and no sesquiterpene lactones (Bohlmann, et al., #239). The isolated position of the genus is supported to the extent that there are no sesquiterpene lactones, but these are lacking in some other Vernoniaeae such as *Piptocarpha*.

Trichospirinae Lessing, *Linnaea* 6: 390. 1831.

Prostrate Herbs with sessile leaves; leaves alternate on vegetative stems, subopposite on fertile stems. Heads axillary, with bracts which represent either compound heads or paleae; corollas ca. 2 mm long, deeply 4-lobed; thecae not caudate; style branches with slender smooth pointed hairs; achenes biconvex, biaristate, covered with papillae. Pollen grains sublophorate, strongly spinose (*Lychnophora*-type).

Type genus: *Trichospira* H.B.K.

The subtribe contains the single genus and species widely distributed in the American tropics at low elevations near coasts and rivers. The species, *T. verticillata* (L.) Blake, has been placed in the Heliantheae-Coreopsidinae in traditional treatments (Bentham & Hooker, 1873; Hoffmann, 1890-1894) because of the biconvex biaristate achenes, but it was returned to the Vernoniaeae by Robinson and Brettell (1973). The achenes remain totally unique within the tribe. The leaves of the fertile branches are often described as opposite, which would be unusual in the Vernoniaeae, but examination shows that they are slightly offset, alternate internodes being greatly abbreviated to give the appearance of leaf-pairs. The pollen is of the unspecialized type that seems primitive in the Vernoniaeae and the genus may represent an isolated divergent line in the tribe.

Cassini (1828) included *Trichospira* in the general group with *Polaria* and *Spiranthes*, and there is some resemblance, especially in the reduced, often 4-lobed corollas, but other details, including achenes and pollen, are so different that close relationship seems unlikely.

The chemistry is not known, but should be of great interest as a test of the relationship.

Lychnophorinae Benth. & Hook., *Gen. Pl.* 2: 171. 1873. emend
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Perennial herbs and shrubs or small caudex-forming trees. Leaves large, or reduced and densely spirally inserted, often with lepidote or sublepidote pubescence. Inflorescence with

heads usually densely clustered or compound, sometimes clustered at end of long scape or forming secondary capitula. Heads usually with 1-5 flowers, rarely to 25 flowers; corolla regular, mostly 5-lobed; achenes sometimes dimorphic in pubescence and pappus (*Lychnophoropsis* and *Pithecoseris*); pappus usually with 2 distinct series, sometimes graduated or uniseriate, longer pappus elements setiform or strap-shaped. Pollen grains sublophorate or lophorate with low crests, strongly spinose (*Lychnophora* and *Chresta* types), mostly 30-40 μ m in diameter.

Type genus: *Lychnophora* Mart.

The subtribal name was superfluous at the time of description because of the inclusion of *Elephantopus* and *Rolandra*, type genera of previously named subtribes. The name Lychnophorinae becomes valid with the removal of the latter elements (Art. 63.3).

The subtribe is considered as including the following genera: *Albertinia* Spreng., *Chresta* Vell. ex DC., *Chromopappus* DC., *Eremanthus* Less., *Lychnophora* Mart., *Lychnophoropsis* Sch.Bip., *Piptolepis* Sch.Bip., *Pithecoseris* Mart. ex DC., *Proteopsis* Mart. & Zucc. ex DC., *Soaresia* Sch.Bip., nom. cons. (*Bipontia* Blake), and *Vanillosmopsis* Sch.Bip. The group is almost entirely restricted to Brasil. *Eremanthus jelskii* Hieron, and *Vanillosmopsis weberbaueri* Hieron., from Peru, do not seem to belong to those genera or to the subtribe.

The Lychnophorinae have traditionally been distinguished by having clustered heads with few flowers per head. The original concept has proven to include two separate lines of development, the Elephantopodinae and Rolandrinae having strongly lophorate pollen and, where known, a chemistry unlike that of the Lychnophorinae as delimited here. Also, the present concept includes some elements in *Piptolepis* and *Eremanthus* that have 12-25 flowers in the heads, and includes the genera *Albertinia* and *Vanillosmopsis* which were placed in a remote position near the beginning of the tribe by Bentham and Hooker (1873) and Hoffmann (1890-94) because of their uniseriate pappus. All members of the subtribe have pollen of the *Lychnophora*-type or of the immediately related *Chresta*-type (Robinson, 1980a). The lophorate condition of the *Chresta*-type is structurally related to the *Lychnophora*-type, and it has no evident relationship to the lophorate forms with high ridges seen in the Vernoniinae, Elephantopodinae, and Rolandrinae.

Recent chemical studies (Bohlmann, et al., #283, 287, 312, 314, 320; Vichnewski, et al., 1976) have shown that members of the Lychnophorinae as presently circumscribed tend to have furanone heliangolides such as goyazensolide, a type of germacranolide not seen in the Vernoniinae or Elephantopodinae. At the same time the Lychnophorinae seem to lack the various non-furanone germacranolides that are common in members of the Vernoniinae or the germacranolide dilactones that are known in the Elephantopodinae. Furanone heliangolides do occur elsewhere in the tribe in the genus *Centratherum* which may be related

to the Lychnophorinae, but which is strikingly different in structure and is placed here in a separate subtribe. The chemistry of *Chresta* shows relationships to that of the Vernoniinae, as both a glaucolide and a hirsutinolide are present.

In the present paper, *Piptolepis* is placed in the Lychnophorinae on the basis of the furanone heliangolides (Bohlmann, et al., #314) and general habit, even though the heads are not densely clustered and have up to 25 flowers per head. *Albertinia* is included on the basis of its evident relationship to *Vanillosmopsis* even though the chemical analysis thus far has found only acyclic squalene and some closely related cyclic triterpenoids. *Vanillosmopsis* previously has been shown to contain eremanthine identical to that in *Eremanthus* (Vichniewski & Gilbert, 1972; Harborne & Williams, 1977), and more recently a furanone heliangolide of the goyazensolide type has been reported (Bohlmann, et al., #314), also linking the genus to *Eremanthus* in the traditional Lychnophorinae.

CENTRATHERINAE subtribus nov., H. Robinson, R.M. King & F. Bohlmann

Plantae herbaceae annuae vel breviter perennes in specie unico fruticosae. Capitula terminalia subsolitaria vel diffuse disposita multiflora non paleacea; squamae involucri dimorphae exteriores foliosae interiores aristatae vel muticae persistentes; corollae 4-13 mm longae regulares 5-lobatae plus minusve longe stipitato-glanduliferae; cellulae endotheciales subquadratae, parietibus in lineis numerosis ornatis; pili stylorum pungentes; setae pappi facile deciduae vel nullae. Grana pollinis irregulariter leniter lophorata spinulosa in diametro ca. 40 μ m (*Centratherrum*-type).

Type genus: *Centratherrum* Cass.

The subtribe contains the genera *Centratherrum* Cass. and *Oiospermum* Less. It is primarily Neotropical, and it contains some Old World elements, but some previously associated Old World elements are excluded. An Asiatic genus *Phyllocephalum* Blume has often been included in *Centratherrum*, being reseggregated only recently by Kirkman (1978, in herb.), but the latter differs by having a strongly lophorate form of pollen close to that called Type F by Keeley and Jones (1979). The latter authors cite the pollen type from Old World species of *Vernonia*, and the genus *Phyllocephalum* is regarded here as a member of the subtribe Vernoniinae.

The corollas of the Centratherinae show few to many long-stalked *Hieraceum*-type glands in all species examined. It is notable that such glands are absent in *Phyllocephalum*, further indicating that the latter is not closely related to *Centratherrum*.

The *Centratherrum*-type pollen is similar to that called the *Chresta*-type by Robinson (1980a), having a distinct lophorate pattern with low ridges. In the Centratherinae, the areoles of the pollen are more numerous and more irregular than in *Chresta*,

often being elongate rather than isodiametric. Both pollen types are closely related to the basic widely distributed *Lychnophora*-type, and are not close to the strongly lophorate pollen types of the Vernoniinae.

Centratherum has been shown to contain furanone heliangolides (Ohno, McCormick & Mabry, 1979; Bohlmann, et al., #289), suggesting relationship to the Lychnophorinae, but the multi-flowered rather solitary heads differ completely from members of that group. The new subtribe cannot be distinguished as easily from the large subtribe Vernoniinae on the basis of structure, but the latter group is more distinct chemically, lacking furanone heliangolides.

PIPTOCARPHINAE subtribus nov., H. Robinson, R.M. King & F. Bohlmann

Plantae fruticosae vel subarborescentes; caules et folia plerumque lepidota vel stellate pilosa. Lamina foliorum a petiolis valde demarcatae. Inflorescentiae pyramidaliter paniculatae vel axillares; squamae involucri interiores facile deciduae interdum in parte connatae; corollae regulares 5-lobatae; thecae antherarum interdum caudatae; pili stylorum breves apice rotundatae in parietibus saepe incrassatae rugulosae interdum septatae; pappus plerumque biseriatus exterior saepe distinctus rebribus interior capilliformis vel taeniatus. Grana pollinis sublophorata valde spinulosa in diametro ca. 40 μm (*Lychnophora*-type).

Type genus: *Piptocarpha* R.Br.

The subtribe is presently recognized as containing three genera, *Piptocarpha* R.Br., *Pollalesta* H.B.K., and *Critoniopsis* Sch.Bip. The genera are notable for their lepidote or stellate pubescence on the stems and leaves, but the most significant character of the group seems to be the short, blunt, often roughened hairs of the styles which can be seen even in the nearly glabrous-leaved *Piptocarpha lushnathii* Kraschen (= *P. stifftioides* H. Robinson, *Stifftia axillaris* Barroso & G. da Vinha). Septate hairs have been illustrated by Cabrera (1944) for *Piptocarpha sellowii* (Sch.Bip.) Blake, and also occur in such species as *Critoniopsis pyenantha* (Benth.) H. Robinson, *C. elbertiana* (Cuatr.) H. Robinson, and some other members of the genus, however, the character is absent in some other species of the subtribe, and it may occur rarely in other subtribes.

Some species of Piptocarphinae closely approach members of the Vernoniine genus *Eremosis* of Mexico and Central America in some characters, but actual relationship may not be close. The subtribe has the primitive *Lychnophora*-type pollen as do the similar members of the Vernoniinae, and they all have apparently evolved from nearer the basal stock of the tribe. The sterile tails on the anthers in *Piptocarpha* are a unique specialization, such tails not being found elsewhere in the tribe.

Chemical data on the subtribe is meager. Extracts of *Piptocarpha oblonga* (Gardn.) Baker include some triterpenes and

flavonoids (Bohlmann, et al., #289). None of the complex germanolides common in other subtribes have been observed.

Vernoniinae Lessing, Synopsis 146. 1832.

Annual or perennial herbs, shrubs, or small trees, few to many branched, glabrous to densely tomentose. Leaves alternate to rarely opposite. Inflorescence solitary, diffuse, cymose, corymbose or thyrsoid-paniculate. Heads with 1-many flowers; involucre bracts multiseriate, inner and outer bracts similar or variously differentiated, bracts with or without appendages or apical aristae; receptacle usually without paleae (with paleae in *Bolanosa* A.Gray, *Lepidonia* Blake of Mexico and Guatemala, *Heterocomma* DC. and *Alcantara* Glaziou ex Barroso of Brasil, and *Dewildermania* O.Hoffm., *Gossweilera* S.M.Moore, and *Omphalopappus* O.Hoffm. of Africa); corollas usually purplish or whitish (yellowish in *Gongrothammus* Steetz; reddish in *Mattfeldanthus* H.Robins. & King), usually 5-lobed, usually regular (ligulate with 5 equal lobes in all except a few central flowers in *Stokesia* L'Hér., bilabiate with 2 longer exterior lobes in *Dipterocypsela* Blake, peripheral flowers with 4 shorter outer lobes in *Mattfeldanthus*); anthers calcarate, not tailed (slightly subcaudate in *Adenoon* Dalz.); endothelial cells mostly quadrate with irregular fine lines on inner surface; anther appendages with or without glands; style with sharp or sometimes a few rounded hairs abaxially, sometimes with glands; achenes prismatic or obcompressed, rarely winged (*Dipterocypsela*), rarely dimorphic (*Heterocypsela* H.Robins.); pappus usually double with short outer series and capillary inner series, sometimes with only capillary setae of various lengths, sometimes reduced to a corona or massive collar (*Struchium* R.Br.). Pollen grains sublophorate (*Lychnophora*-type) to strongly lophorate with various patterns of high crests, rarely with crests having exposed columellae (*Phyllocephalum*), with small to large spines, mostly 30-60 μ m in diameter.

Type genus: *Vernonia* Schreb., nom. cons.

The subtribe includes the vast majority of the genera and species of the tribe and ranges geographically throughout the Old World tropics and American tropics extending northward into eastern North America. The subtribe includes those elements of the tribe that share the commonest and most functional character-states and most of these have been placed in the genus *Vernonia* sensu lato. Such combinations of character-states probably approximate the ancestral condition in the tribe, but *Vernonia* sensu lato probably represents many parallelisms, and probably includes a mixture of both primitive and specialized forms. For this reason reference is given here to segregate genera of *Vernonia*, especially in the Old World where the species differ chemically and cytologically from the type *V. novaboracensis* (L.) Michx. of eastern North America.

The Vernoniinae have a complete range of variation in pollen form (Stix, 1960), including the *Lychnophora*-type or Type A

which seems to be primitive (Keeley & Jones, 1979), and various strongly lophorate types that seem to be derived. All variations seem to be potentially useful in taxonomy, but the various lophorate types differ from each other in less significant details in the patterns. In the latter case definite parallelisms and some cases of variations between species that must be rather closely related have been seen (Robinson, 1980b). The difference between the lophorate and the *Lychnophora*-type seems more basic, and examples of differences within closely related groups are less obvious. The "Lepidaploae scorpioideae" group of *Vernonia* in Baker (19873) contains many species under the part called "subscorpioideae" with various lophorate pollen types, and many under the part called "scorpioideae verae" with the *Lychnophora*-type, but more recent studies indicate these groups of species are not closely related (Robinson, 1980b). In Africa, typical members of *Baccharoides* Moench have lophorate pollen, but some species treated as a subgroup by Smith (1971) have *Lychnophora*-type pollen. In the latter case, differences in other characters make actual relationships between *Baccharoides* and its simulators uncertain.

Genera of the Vernoniinae in both Hemispheres with *Lychnophora*-type pollen such as typical *Vernonia* of eastern North America, the "scorpioideae verae" Baker of tropical America, *Eremosia* (DC.) Gleason and *Leiboldia* (Schlecht. ex Benth. & Hook.) Gleason of Mexico and Central America, the monotypic *Hololepis* DC., *Heterocoma* DC., and *Alcantara* Glaziou ex Barroso of Brasil, and *Gymnanthemum* Cass. and *Gongrothamnus* Steetz (*Grogonothamnus* of some authors) of Africa would seem to present more primitive pollen states for their areas, but the extent of independent origin of the lophorate forms in the two Hemispheres remains in question. The pollen of typical *Baccharoides* in Africa, seems identical with forms in *Stokesia* L'Hér. of the southeastern United States, and *Vernonia* subg. *Lepidaploa* Cass. (lectotype: *Vernonia albicaulis* Pers.), *Pacourina* Aubl., and *Struchium* P. Browne of tropical America, but the lophorate pollen in *Cyanthillium* Blume in eastern Asia and Malaysia seems different. The lophorate types "E" and "F" of Keeley and Jones (1979), in which the ridges of the reticulum have exposed columellae, are apparently restricted to the Old World.

In other respects the Vernoniinae of America and the Old World seem to represent distinct groups. The basic chromosome number of many Old World segregates of *Vernonia* seems to be $X=10$ while the American groups have mostly $X=17$ (Jones, 1977). Old World genera have a distinct sesquiterpene lactone chemistry: elemanolides have been reported from species of *Baccharoides* and *Cyanthillium* and vernolide type germacranolides have been reported in *Baccharoides*, *Gymnanthemum*, and *Cyanthillium* (Lleander-Chanco, Herrera & Balgos, 1976; Harborne & Williams, 1977). These forms do not occur in American Vernoniinae. The American genera tend to have various glaucolides or hirsutinolides

(Harborne & Williams, 1977; Bohlmann, et al., 1979, #296), which are present also, however, in some Old World species that have been placed in *Vernonia*, and in an African species of *Erlangea* (Bohlmann & Czerson, 1978). Old World Vernoniinae tend to be different in flavonoid chemistry also, having only flavone glycosides, while American taxa have either flavones, flavanols, or both.

Taxonomically useful chemical data on the subtribe Vernoniinae is available from many sources, and the general summary by Harborne and Williams (1977) can be consulted for some of the more significant correlations. Epoxy fatty acids are widely distributed in the tribe, but seem most abundant in *Stokesia* and species of *Baccharoides* of the Vernoniinae, both of which have been studied as possible commercial sources (Gunn & White, 1974; Smith, 1971). Harborne and Williams (1977) recognize the systematic limitations of the epoxy resins, however, since they are neither present in all Vernonieae nor are they restricted completely to the tribe. *Stokesia* also contains hirsutinolides similar to those in American species of *Vernonia*, indicating relationship to the latter.

Three African genera, *Erlangea* Sch.Bip., *Ethulia* L.f., and *Bothriocline* Oliv. ex Benth, & Hook. seem to be linked by the occurrence of distinctive 5-methylcoumarins (Rustaiyan, et al., 1980b). The first of these also contains highly oxygenated germacranolides similar in some ways to those in *Baccharoides*, *Cyanthillium*, and *Gymnanthemum* (Rustaiyan, et al., 1980a).

Other chemicals seem useful in taxonomy of the Vernoniinae at a more restricted level. Allenic germacranolides have been isolated from *Vernonia cotoneaster* Less and *V. lilacina* Mart., two distinct but related members of the subgenus *Lepidaploa* (Bohlmann, et al., #292, 296). Elaborated acyclic sesquiterpenes of a type not previously known in the tribe have been isolated from *V. polyanthes* Less. and *V. fagifolia* Gardn., two of the non-scorpoid members of the "scorpioideae verae" (Bohlmann, et al., #296).

Elephantopodinae Lessing, *Linnaea* 5: 135. 1830.

Perennial herbs from stolons or rootstocks. Inflorescence corymbose to spicate or glomerulate; heads usually clustered, or compound with clusters often subtended by 1-many foliaceous bracts; involucre of 4 pairs of bracts; flowers mostly 2-4; corollas 4-10 mm long, unequally 5-cleft. Pollen grains strongly lophorate, with high smooth crests.

Type genus: *Elephantopus* L.

The group has been recognized at the subtribal level by Cabrera (1944) and Cabrera and Vittet (1961) in include three genera, *Elephantopus*, having a pappus of 5 straight awns or setae, *Orthopappus* Gleason with numerous straight pappus setae, and *Pseudelephantopus* Rohr with distorted pappus setae. The group was distinguished by the zygomorphic corollas having the

inner cleft much deeper than the others. The group has since been treated for the North American, Central American, West Indian area with *Elephantopus* interpreted broadly to include the other two genera (Clonts & McDaniel, 1978).

The strongly lophorate pollen grains with high crests seem to relate this subtribe and the following Rolandrinae to the more advanced members of the Vernoniinae, and there is no reason to place them close to the Lychnophorinae with which they were placed in the traditional treatments of Bentham and Hooker (1873) and Hoffmann (1890-94).

Elephantopus has been chemically analysed and seems to have a tendency for sesquiterpene dilactones, a tendency not seen elsewhere in the tribe (Harborne & Williams, 1977). The group has no indication of the furanone heliangolides which seem characteristic of most Lychnophorinae, further emphasizing the lack of relationship between the two groups.

Rolandrinae Lessing, *Linnaea* 6: 105. 1831.

Perennial herbs and shrubs. Heads in axillary or pedunculate clusters or glomerules, each head with 1 flower; involucre bracts 2-6, with apical spur or arista; corollas ca. 2 mm long, regular, with 4-5 lobes, lobes with sclerified tips externally; pappus of short squamellae. Pollen grains strongly lophorate, with high crests bearing small spinules.

Type genus: *Rolandra* Rottb.

The subtribe contains the genera *Rolandra* and *Spiracantha* H.B.K. of Central America and northern South America. The subtribe shares clustered heads and strongly lophorate pollen with the Elephantopodinae with which it is placed in the traditional systems of Bentham and Hooker (1873) and Hoffmann (1890-94), and it probably shares an origin with that group from advanced members of the subtribe Vernoniinae. The technical difference from the Elephantopodinae is the actinomorphic corolla, but the two genera of the Rolandrinae also have single flowers in the head and corollas of reduced size with sclerified lobe-tips. Further examination of these and other genera may show that a broader subtribal concept is preferable.

Chemistry of the Rolandrinae is not yet known.

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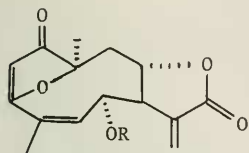
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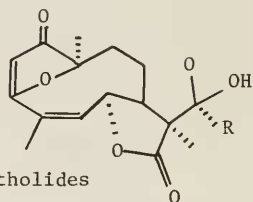
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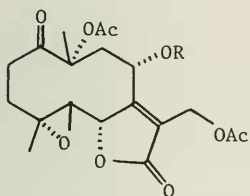
Sesquiterpene lactones



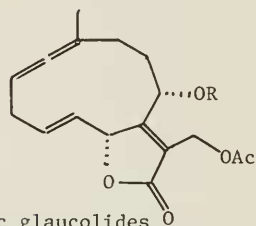
goyazensolides



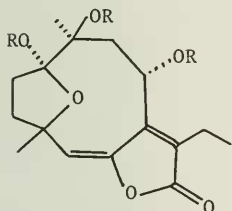
eremantholides



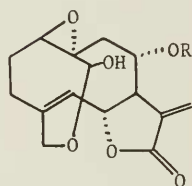
glaucolides



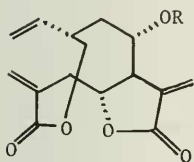
allenic glaucolides



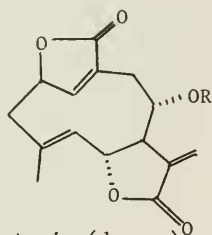
hirsutinolides



vernolides

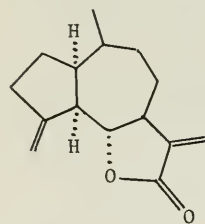


vernolepin type



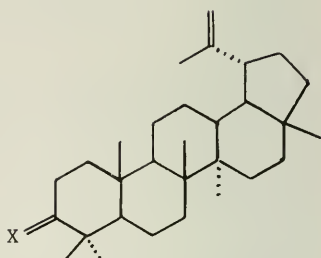
elephantopin (desoxy)

Sesquiterpene lactone

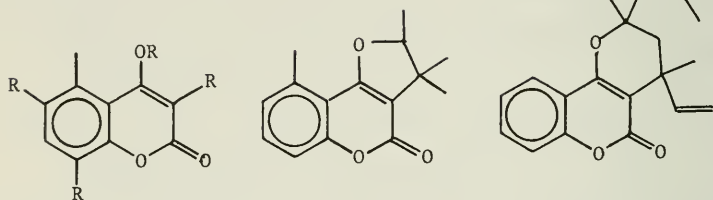


guaianolides

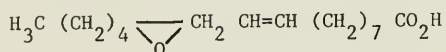
Triterpene



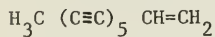
Coumarins



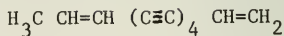
Epoxy fatty acid



Polyacetylenes



pentaynene



trideca-1,11-diene-3,5,7,9-tetrayne

Main chemical constituents of the tribe Vernonieae - II